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# Orthonormal Transform to Decompose the Variance of a Life-History Trait Across a Phylogenetic Tree

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Summary. In recent years, there has been an increased interest in studying the variability of a quantitative life history trait across a set of species sharing a common phylogeny. However, such studies have suffered from an insufficient development of statistical methods aimed at decomposing the trait variance with respect to the topological structure of the tree. Here we propose, a new and generic approach that expresses the topological properties of the phylogenetic tree via an orthonormal basis, which is further used to decompose the trait variance. Such a decomposition provides a structure function, referred to as "orthogram," which is relevant to characterize in both graphical and statistical aspects the dependence of trait values on the topology of the tree ("phylogenetic dependence"). We also propose four complementary test statistics to be computed from orthogram values that help to diagnose both the intensity and the nature of phylogenetic dependence. The relevance of the method is illustrated by the analysis of three phylogenetic data sets, drawn from the literature and typifying contrasted levels and aspects of phylogenetic dependence. Freely available routines which have been programmed in the R framework are also proposed.

Key words: Life history trait; Orthogram; Orthonormal transform; Phylogenetic tree; Variance decomposition.

## 1. Introduction

In recent years, there has been considerable interest in analyzing the variability of one or several life-history traits, expressed as quantitative variables, across a set of species sharing a common phylogeny. Such studies find their justification in the "comparative method" (Harvey and Pagel, 1991), which provides a renewed and enlarged vision of an old and central paradigm of natural sciences. Comparative studies have investigated the way in which two life-history traits may correlate across a phylogenetic tree, as well as the correlation between one trait and an environmental variable. A serious statistical problem, affecting all these studies, arises from the fact that species that are part of a hierarchically structured phylogeny cannot be a priori considered as independent observations of a life-trait variable (Felsenstein, 1985). Very often the presence of "phylogenetic signal" (Blomberg, Garland, and Ives, 2003) also called "phylogenetic autocorrelation" (Gittleman and Kot, 1990) is to be expected which means, for instance, that the difference in trait values observed for a given pair of species is likely to depend on their relative position in the phylogenetic tree.

The potential dependence of the values taken by the trait in relation to the topological structure of the phylogenetic tree, that is, "phylogenetic dependence," deserves great interest, not only because it may violate the main assumptions on which current statistical tests are built, but also because a proper characterization may provide valuable insights into the processes and mechanisms that have shaped the data under consideration. This has long been acknowledged (Gittleman and Kot, 1990) in a trend analogous to the increased interest for the study of temporal and/or spatial dependence that has been observed in ecological sciences (Legendre, 1993).

However, concepts and methods originating from time-series analysis and spatial statistics proved to be of a more direct applicability to ecological data than to phylogenetic topics. Central to these methods are "structure functions" (Legendre and Legendre, 1998), such as correlogram, variogram, periodogram (Ripley, 1981; Cressie, 1991; Wackernagel, 2003) or wavelet-based "scalograms" (Percival and Walden, 2000), which are useful to describe models and test spatial or temporal patterns. Graphic tools (e.g., more or less sophisticated geographical maps) are also widely used as complements of the summary provided by structure functions. In contrast to this well-established, yet still burgeoning, field developments addressing the description of phylogenetic dependence have remained limited. Many tests dealing with phylogenetic issues have been proposed (Blomberg, et al., 2003), several of them addressing the significance of the correlation between a trait variable and the phylogenetic tree. But there is no method providing a satisfactory description of how the variance of a quantitative variable is distributed along a phylogenetic tree. In particular, the application of nested analysis of variance (Bell, 1989) cannot completely accommodate full phylogenetic information (Blomberg

et al., 2003), while the only published structure function is an extension to phylogeny of the correlogram concept (Gittleman and Kot, 1990), which is far from having optimal properties (Rohlf, 2001), just as the usual correlogram is generally not the most relevant structure function to address spatial or temporal dependence (Ripley, 1981). In addition, the lack of graphical standards is blatant in the literature devoted to phylogeny, in which simultaneous displays of trait values and of the reference phylogenic tree are very scarce.

The main object of this article is to provide a canonical procedure to decompose the variance of a life-trait variable with respect to the topological structure of a phylogenetic tree, and to propose a new structure function, called an "orthogram," to express such a decomposition on an orthonormal basis constructed from the topology of the tree. Additionally, we intend to provide some complementary nonparametric test statistics derived from the orthogram, along with principles for a simultaneous graphical display of both trait values and phylogeny. The effectiveness of the approach will be illustrated and compared with the phylogenetic correlogram, using examples drawn from the literature and showing contrasted patterns of phylogenetic dependence.

## 2. An Orthonormal Basis to Decompose Trait Variance

### 2.1 *Building an Orthonormal Basis from the Topological Structure*

Let us consider a life-history trait represented by a quantitative variable $\mathbf{x} = (x_1, \ldots, x_t)^T$ measured on $t$ taxonomic units, for which the topology of the phylogenetic tree is assumed to be a priori fully determined. We will consider the following terminology concerning the phylogenetic tree. The root is the common ancestor to all the $t$ contemporary taxons (OTUs: operational taxonomic units, also called "tips") and to the $n$ hypothetical nodes (HTUs: hypothetical taxonomic units); branches emanate from root and nodes, tracing the course of evolution. Phylogenetic trees used by biologists are generally "consensus trees" (Adams, 1972) or "super-trees" (Sanderson, Purvis, and Henze, 1998) obtained by compiling phylogenies established by distinct methods, which means that branch lengths are often unknown or not accurate.

Even when data are from homogeneous origins, the estimation of distances between tips from either fossil, morphological, or molecular data relies on the hypothesis that all traits evolve at a steady rate along all branches. But evolutionary rates are known to change with time (Svensson, 1997) while varying between branches of a phylogenetic tree (Mindell and Thacker, 1996) and this often introduces a substantial level of uncertainty around estimates of branch lengths. Consequently, we will restrict ourselves to the most general type of data for which only the topological structure of the phylogenetic tree, that is, the relationships among nodes and between nodes and tips, can be assumed to be known.

Each taxonomic unit of the tree (either tip or node) defines a set made of its descendant tips. Thus, we can associate a dummy variable $\mathbf{u}^k = [u_i]^k_{1 \le i \le t}$ to each taxonomic unit $k$ (including the root, $1 \le k \le n + t + 1$), with $u_i^k = 1$ if the tip $i$ is descended from that taxonomic unit $k$, and $u_i^k = 0$ otherwise. For example, the node N2 in Figure 1A defines a subset of tips which is {L7, L8, L9, L10, L11, L12}, while the corresponding dummy variable is $\mathbf{u}^T = (0, 0, 0, 0, 0, 0, 1, 1, 1, 1, 1, 1)$. For the subsequent analyses, we need to define a relative order between dummy variables and, thus, between the corresponding taxonomic units (TU). A reasonable quantitative criterion to rank the TU is the number, $np(k)$, of permutations between descendants of a given node $k$ that preserve the topological structure of the subtree stemming from it. With such a criterion, nodes are ranked according to the complexity of the subtree they initiate. Let us now consider the table $\mathbf{U} = [\mathbf{u}^k]$ that contains the whole sets of the dummy variables.

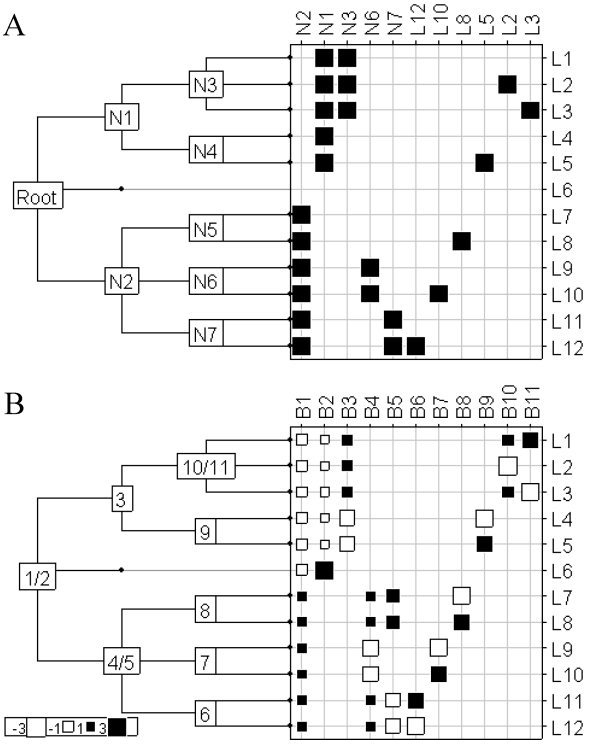


**Figure 1.** Illustration of the orthonormal basis construction from a fictive phylogenetic tree featuring 12 tips and 7 nodes. (A) Representation of $t - 1$ dummy variables, associated to nodes and tips, and ordered by decreasing values of $np$ (names of the dummy variables are labeled on the top of the table). (B) Representation of the $t - 1$ orthonormal vectors of the orthonormal basis $\mathbf{B}$. For each node of the phylogeny, the labels indicate which vectors account for the variance associated to each node. The size of the squares is proportional to the values of the orthonormal vectors (white and black for negative and positive values, respectively).

All these dummy variables are obviously not linearly independent. The most obvious reason is that the dummy variables corresponding to the direct descendants of a given node, $k$, sum to the dummy variable, $\mathbf{u}^k$. This problem can be easily resolved by suppressing for each node, $k$, the dummy variable corresponding to its direct descendant displaying the lowest $np$ value. This means eliminating $n + 1$ dummy variables (the root is considered as a node) among the $n + t + 1$ possible, that is, retaining only $t$ of them. The next step is a rowwise concatenation of these $t$ dummy variables to form a $t \times t$ matrix, $\mathbf{V}$ (Figure 1A). The QR decomposition (Harville, 1997)

of matrix $\mathbf{V}$ yields a $t \times t$ matrix, $\mathbf{Q}$, whose columns are the orthogonal vectors obtained by applying Gram–Schmidt orthogonalization to the columns of $\mathbf{V}$.

The orthonormal basis $\mathbf{B}$ associated with the phylogeny is defined from the orthogonal basis $\mathbf{Q}$. We eliminate the first vector $\mathbf{1}_t$ corresponding to the dummy variable attached to the root and we standardize by $t^{1/2}$ to obtain $t-1$ orthonormal vectors (Figure 1B). Orthonormality guarantees that $\frac{1}{t}\mathbf{B}^T\mathbf{B} = \mathbf{I}_{t-1}$. The vectors of $\mathbf{B}$ are linear combinations of the dummy variables, and the Gram–Schmidt orthogonalization guarantees that each of these vectors is ranked in accordance with the initial ranking of the dummy variables. Consequently, the first vectors will characterize interspecific variance among dissimilar species (two species are all the more dissimilar that the *np* value of their first common ancestor is high) and reciprocally. This enables an interpretation of the successive vectors in terms of decreasing phylogenetic dissimilarity between tips.

### 2.2 *Decomposition and Reconstruction of the Life-Trait Variable*

From the orthonormal basis $\mathbf{B}$, we can compute a vector $\mathbf{r} = (r_1, \ldots, r_{t-1})^T$ of the transform coefficients of the centered and standardized variable $\mathbf{x_0}$, as $\mathbf{r} = \frac{1}{t}\mathbf{B}^T\mathbf{x_0}$. Centering and standardizing are carried out using the uniform weighting of tips. Standardization allows us to have cumulated orthogram values between 0 and 1 thereby facilitating comparisons between examples.

Transform coefficients allow one to reconstruct the variable using $\mathbf{x}_0 = \mathbf{Br}$, while squared-transform coefficients provide a decomposition of its variance: $\|\mathbf{x_0}\| = \frac{1}{t}\mathbf{x_0}^T\mathbf{x_0} = \frac{1}{t}\mathbf{r}^T\mathbf{B}^T\mathbf{Br} = \mathbf{r}^T\mathbf{r}$. Squared coefficients, that is, $(r_i^2)_{1\le i\le t-1}$, as well as cumulative squared coefficients, can be plotted against $i \in \{1, \ldots, t-1\}$ yielding two graphical tools, that we will call orthogram and cumulative orthogram, respectively. The sign of coefficients can also be mentioned for orthogram values (see Figures 2–4). Both types of orthograms provide a means to display the variance decomposition for the trait while enabling several tests for phylogenetic dependence. As we will see in the examples, the ordering of orthonormal vectors by decreasing *np* values of the corresponding dummy variables enhances the interpretability of orthogram results.

## 3. Testing for Phylogenetic Dependence

We consider as null hypothesis ($H_0$) the complete absence of phylogenetic dependence (Bloomberg et al., 2003) and, thus, that the $t$ observed tip values are exchangeable irrespective of the topological structure of the tree. This means that the observed decomposition of the trait variance is to be compared with decompositions obtained from a sample of the $t!$ permutations defined on the elements of $\mathbf{x} = [x_i]_{1\le i\le t}$, and for which the orthogram is expected to have uniform values. To carry out such a comparison, we introduced four statistics computed from the variance decomposition on which tests of the null hypothesis are based. The four tests are complementary in the sense that they may have different relevance and power in the presence of distinct alternatives to $H_0$ (see below).

A first test is built on the statistic,

$$\text{R2Max}\,(\mathbf{x}) = \max\left(r_1^2, \ldots, r_{t-1}^2\right),$$

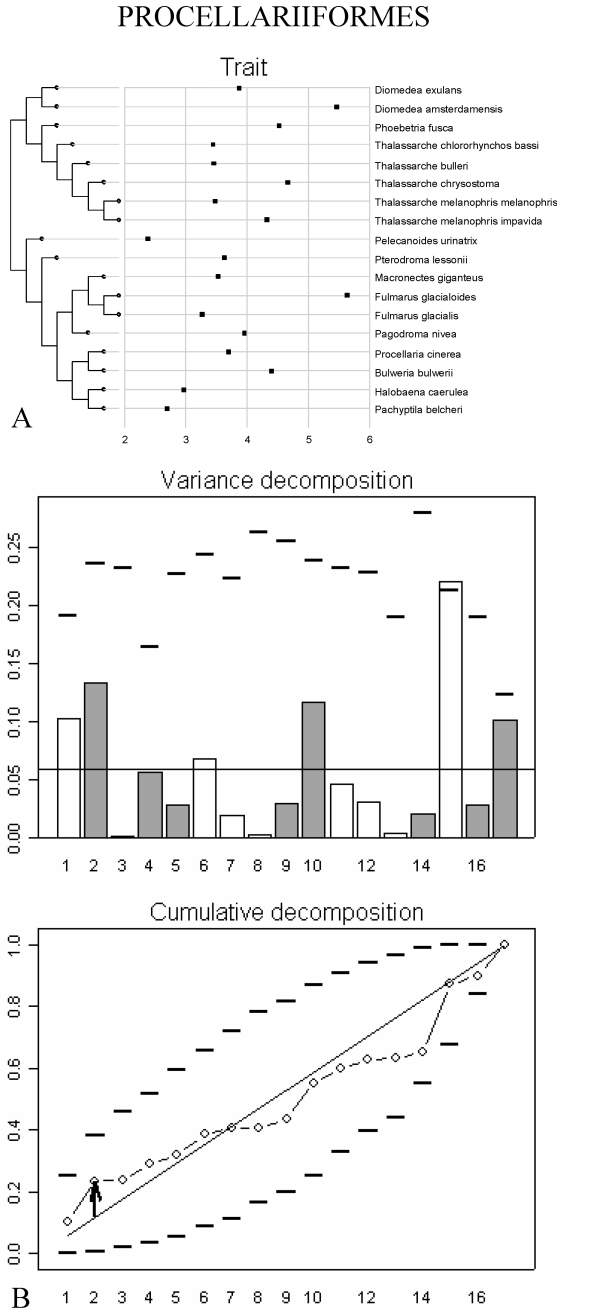


**Figure 2.** Analysis of the adult life expectancy for 18 species of procellariiformes (Bried et al., 2003). (A) Phylogenetic tree (on the left) with dotplot of the life expectancy variable (center) and species names (on the right). (B) Orthogram and cumulative orthogram plots. Orthogram plot: the bars are proportional to the squared coefficients (white and gray bars stand for positive and negative coefficients, respectively). The dashed line is the upper confidence limit at 5%, deduced from 999 Monte Carlo permutations (mean value indicated by the horizontal solid line). Cumulative orthogram plot: circles represent observed values of cumulated squared coefficients, expected values under $H_0$ are along the straight line, and dashed lines stand for the bilateral confidence interval.

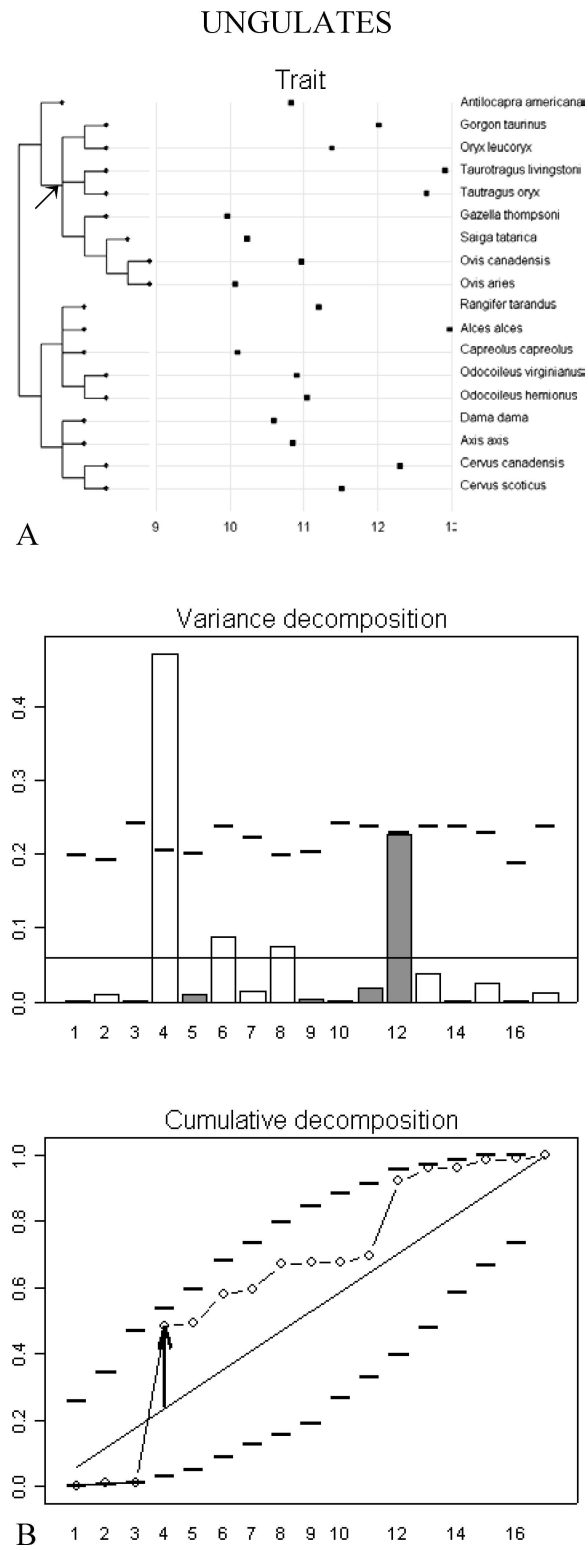


**Figure 3.** Analysis of the adult female body weight (afbw) of 18 species of ungulates (Pélabon et al., 1995). (A) Phylogenetic tree (on the left) with dotplot of the adult female body weight (center) and species names (on the right). (B) Orthogram and cumulative orthogram plots (see the legend of the Figure 2 for explanations).

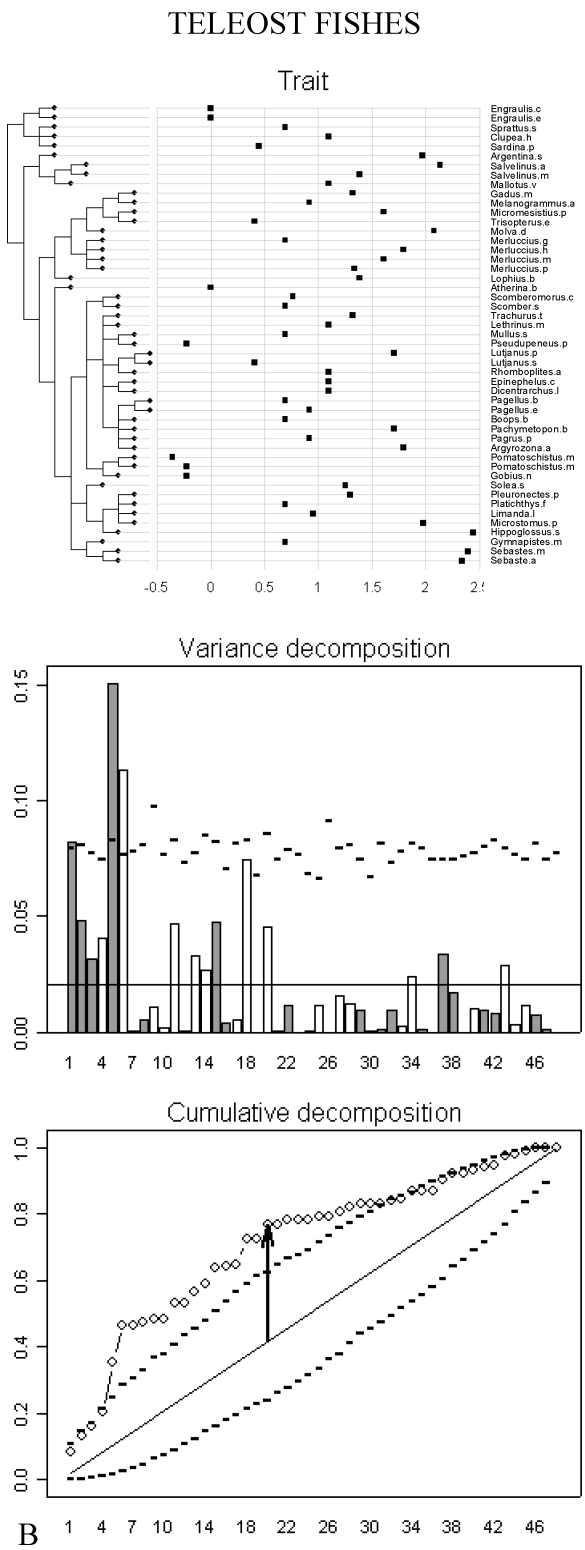


**Figure 4.** Analysis of the age at maturity (years) of 49 species of teleost fishes (Rochet et al., 2000). (A) Phylogenetic tree (on the left) with dotplot of the age at maturity (center) and species names (on the right). (B) Orthogram and cumulative orthogram plots (see the legend of the Figure 2 for explanations).

which is expected to peak when a unique vector of the basis accounts for a large share of the trait variance. This would mean that a significant change in the life trait appeared at one node of the phylogenetic tree while being conserved in the deriving branches. This test is likely to be of limited relevance in the presence of a diffuse dependence, that is, when several nodes are prominent to explain the trait variance and when the orthogram is, therefore dominated by several large values instead of a unique sharp peak. In an analogy with what has been proposed to test smooth periodograms (Bartlett, 1954), we derived a second statistic from the cumulative orthogram, namely,

$$D\max(\mathbf{x}) = \max_{1\leq m\leq t-1}\left(\sum_{i=1}^{m} r_i^2 - \frac{m}{t-1}\right).$$

It corresponds exactly to the Kolmogorov–Smirnov statistic used to test whether the vector $[\sum_{i=1}^{m} r_i^2]_{1\leq m\leq t-1}$ may be an ordered random sample from the uniform distribution on (0, 1). The third test is built on the statistic,

$$\mathrm{SkR2k}(\mathbf{x}) = \sum_{i=1}^{t-1} i r_i^2,$$

which assesses to what extent the variance distribution across the phylogenetic tree is rather skewed to the root or to the tips. The last test corresponds to the statistic,

$$\mathrm{SCE}(\mathbf{x}) = \sum_{i=1}^{t-1}\left(r_i^2 - r_{i-1}^2\right)^2,$$

which measures the average local variation of the orthogram values.

For all four statistics, confidence envelopes are built from a relevant number of Monte Carlo randomizations of the $x_i$ values. All computations and graphical displays involved in the preparation of this article were carried out using R (Ihaka and Gentleman, 1996), with both pre-programmed and personal routines. These routines will be incorporated in the ade4 package available at `http://cran.r-project.org/`, and in the meantime are available by a simple request to the first author. The computer code is available at the Biometrics website `http://www.tibs.org`.

## 4. Applications

Phylogenetic examples came from several papers that studied the degree to which phylogenetic history has shaped the evolution of phenotypic characters or life traits. We retained three examples that typify contrasted levels and aspects of phylogenetic dependence. For each example we compared the results provided by the orthogram with the results yielded by the only other proposed structure function, namely the phylogenetic correlogram (Gittleman and Kot, 1990). The correlogram corresponding to each example is constructed by computing Moran's I coefficients (Cliff and Ord, 1981), for successive classes of phylogenetic distance (Figure 5). Detailed procedures for computing correlogram values and their corresponding confidence intervals are provided by Gittleman and Kot (1990).

Exploratory analyses of life-trait evolution should start with meaningful displays of the variation of the focal trait

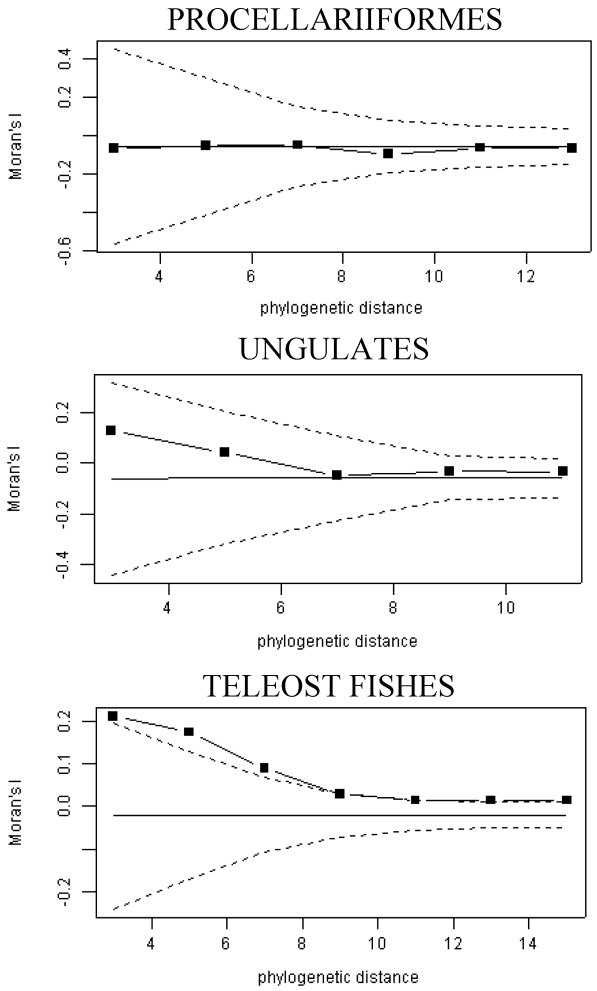


**Figure 5.** Phylogenetic correlograms with respectively six, five, and seven successive Moran's I coefficients (solid squares). The straight line indicates the expected value under $H_0$ and dashed lines the bilateral confidence interval at 5%, deduced from 999 Monte Carlo permutations.

along the phylogenetic tree, just as most quantitative studies of spatially structured phenomena usually start with a visual analysis using geographical maps of the variables under study. But such displays are still greatly lacking in phylogenetic literature and we have, therefore, proposed a simple graphical method. We represent the tree in front of the dotplot of the variable (Figure 2A). This graphical representation takes a leaf out of Cleveland's book (1994) for it was he who defined the dotplot "as a graphical method for measurements that have labels." As for geographical maps in the spatial domain, this graphical representation will help to give a first idea about the nature of the patterns, while enhancing the interpretation of quantitative results.

1. Absence of phylogenetic dependence

We first analyzed data provided by Bried, Pontier, and Jouventin (2002), about the adult life expectancy of 18 species of procellariiformes (Figure 2A). Phylogenetic relationships were compiled from various information sources available for Procellariiformes (see Bried et al., 2002 for details).

**Table 1**
*Observed values and p-values* (*just below*) *for the four test statistics* (999 *Monte Carlo permutations of tip values*)

| | R2Max | SkR2k | Dmax | SCE |
|---|---|---|---|---|
| Procellariiformes | 0.22 | 9.28 | 0.12 | 0.09 |
| | p = 0.27 | p = 0.5 | p = 0.5 | p = 0.12 |
| Ungulates | 0.47 | 8.35 | 0.25 | 0.28 |
| | p = 0.01 | p = 0.3 | p = 0.16 | p = 0.33 |
| Teleost fishes | 0.15 | 15.4 | 0.3 | 2.14 |
| | p = 0.13 | p = 0.001 | p = 0.005 | p = 0.001 |

Because divergence times between species are far from certain (Pontier, personal communication), lengths of branches are considered as unknown. The trait variable of life expectancy has been square root transformed prior to analysis so as to make its distribution more symmetric and normal. None of our four tests rejected the null hypothesis of a uniform distribution of orthogram values, because the observed values of the four corresponding statistics were all exceeded by results of many Monte Carlo randomizations (Table 1). Furthermore, values of the cumulated orthogram remained within the confidence envelopes (Figure 2B). All these results pointed to an absence of phylogenetic dependence for that life-history trait. The phylogenetic correlogram of observed data (Figure 5) also indicated an absence of phylogenetic dependence whatever the distance class. Thus, this example supports the idea that not all traits are correlated to their phylogenetic history. Indeed, there exist specific evolutionary scenarios (Blomberg et al., 2003) under which correlation between a trait and its phylogenetic history is likely to be low. Although testing for the absence of phylogenetic dependence could appear trivial, it is a first and unavoidable step to study the relationship between a life trait and a phylogeny, as shown by this example.

2. Importance of a particular node

For this example, we analyzed a data set from Pélabon et al. (1995) relating to the adult female body weight of 18 species of Ungulates, using their tip data and the joint phylogeny (Figure 3A). Because the phylogenetic relationships are unknown for ungulates (Gaillard, personal communication), a taxonomy-based phylogeny with unknown branch lengths has been used. The trait has been log-transformed prior to analysis. Only the test based on R2Max was significant (Table 1). Moreover, the plot of orthogram values highlighted the prevalence of the fourth vector of the basis, which corresponds to the node highlighted by an arrow on the Figure 3B. The simultaneous representation of that score and trait values (Figure 3A) clearly confirmed the presence of an important evolutionary event that appeared at node w10 and conserved until present. Such an evolutionary pattern generates a kind of phylogenetic dependence that appeared hard to detect by three of the test statistics (SkR2k, DMax, and SCE), by the cumulative orthogram, and also by the phylogenetic correlogram (Figure 5). Only the multiple tests on individual values of the orthogram and the test statistic R2Max proved able to indicate a significant departure from phylogenetic independence.

3. Diffuse phylogenetic dependence

The last example analyzed deals with the age at maturity (years) of 49 species of teleost fishes (Figure 4A). Data have been provided by Rochet et al. (2000) who compiled the most recent information available for teleost fishes to establish phylogenetic relationships. Partial phylogenetic trees based on morpho-anatomical characters and on molecular traits were collated to yield a consensus tree summarizing present knowledge about teleost interrelationships. As data were obtained from different sources and methods, estimates of branch lengths are not available or comparable. The life trait was log-transformed prior to the analysis. This trait can be considered as shaped by phylogenetic history because three test statistics (SkR2k, DMax, and SCE) revealed a significant departure from $H_0$ (Table 1) while the cumulative orthogram had most of its values outside the confidence envelopes (Figures 4B). This pattern of phylogenetic dependence is radically different from the preceding pattern. In this example, the values of the orthogram and, thus, the portions of interspecific variance, decreased regularly as a function of the complexity value, *np*, of the nodes. The phylogenetic correlogram (Figure 5) confirmed the existence of a "phylogenetic gradient": there was a monotonic decrease of coefficients in relation to phylogenetic distance. This profile indicated that closely related species tend to have similar trait values and that such a similarity decreases with phylogenetic distance.

## 5. Discussion

The above examples demonstrate that orthonormal transform is a relevant approach to diagnose different degrees and types of phylogenetic dependence in both small and large phylogenies, as well as with different types of phenotypic characters. The approach is all the more relevant in that modern computer technology with its high-power graphic screens displaying multiple, linkable windows allows one to consider dynamic simultaneous views on the phylogenetic data and on the distributions of the values taken by the structure functions and test statistics.

Characterizing phylogenetic dependence using an orthonormal transform comprises two main steps, namely (i) the definition of an orthonormal basis **B**, which ensures a canonical description of the tree topology and (ii) the variance decomposition on the basis that yields the *structure functions* called orthograms. Such a strategy is generic in the sense that it does not necessitate any assumption on the structure of the tree and therefore contrasts with several ad hoc methods that have been previously proposed. Furthermore, the principle of orthonormal transforms obviously surpasses the study of phylogenetic data. Indeed, in the spatial and/or temporal domain, the Fourier transform as well as several kinds of wavelet transforms (Percival, 2002) also rely on specific orthonormal bases (Percival and Walden, 2000). Furthermore, all the canonical bases associated with linear and bidimensional supports such as the eigenvectors of a graph matrix (Cvetkoviv, Doob, and Sachs, 1979) could be used to calculate spatial and temporal orthograms. Thus, the eigenvectors of a matrix of inter-tips phylogenetic distances (*sensu* Rohlf, 2001) can provide an alternative way to compute a phylogenetic orthogram.

Consequently, the four tests statistics we have used can also be applied to structure functions that are analogues of the orthogram. Statistics R2Max and Dmax have long been

proposed for the Fourier periodogram (Bartlett, 1954; Diggle, 1990), but they are obviously relevant in regards to wavelet decompositions using an orthonormal basis. This is also true with respect to the third and the fourth statistics whose use in relation to structure functions is new to our knowledge. There are, indeed, many extensions of this work, which should be examined in the future. As with so many tests aimed at pattern detection, no information on power is yet available. The three examples we did provide as illustrations cannot claim to encompass all the diversity of phylogenetic patterns, though they clearly illustrate that the different statistics and structure functions are likely to be of varying pertinence and power when facing contrasted alternatives to phylogenetic independence (see in Figures 3 and 5 the limited power of both phylogenetic correlogram and cumulative orthogram with respect to the second example). The orthogram provides a very rich account of variance decomposition because there are as many values as tips (minus 1) in the tree, while the correlogram only gives averaged results for a limited number of classes of phylogenetic distances. This is analogous to the limitation encountered in the temporal/spatial domain with the correlogram (or the closely related Moran's Index, Cliff and Ord, 1981), when compared with a wavelet decomposition that can also provide results for individual observations.

In the future, the different properties of structure functions and test statistics could be useful to identify which kind of phylogenetic dependence is present (e.g., diffuse vs. structured by particular nodes) by considering which particular tests reject the null hypothesis and those which do not. However, in order to do so on a properly established basis it is still necessary to study and assess the power of these tests with regards to phylogenetic data, simulated under various models of evolutionary change, and having contrasted characteristics in terms of branch lengths and divergence time. Moreover, the ultimate goal of most comparative studies being the analysis of the evolutionary patterns of several life traits (Felsenstein, 1985), a multivariate extension of our orthonormal basis approach is, obviously, the next step to consider in the near future.

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